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Ecology of the Belizean black howler monkey (*Alouatta pigra*): a comparison between two populations living in a riparian forest and on coastal limestone hills

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Abstract

This study reports on the ecology of the Belizean black howler monkey (*Alouatta pigra*) in two different habitats. Monkey River is a riparian secondary forest whereas Runaway Creek Nature Reserve (RCNR) is a primary and mature forest situated in a limestone karst hills landscape. This type of ecosystem, neither the population inhabiting this reserve, has been studied before. We contrasted food availability, diet, group size and composition, population density, home range size and activity patterns between those two populations. We predicted the disturbed riparian forest to have higher food availability but a less diverse diet with a higher consumption of fruits. Thus, we predicted howlers to have higher population density, larger groups with more males and more infants, smaller home ranges with more overlapping. Also, we predicted activity budget to be biased toward a less active lifestyle with less travel but more inactivity, and more social interactions. Our results confirm some of those predictions as food availability is higher in Monkey River with food species accounting for 80% of the diet and all food species of howlers diet having a higher total relative basal area. This is likely to be associated with the higher population density (44.82ind/km² in Monkey River against 26in/km² in RCNR) and smaller average home range size (3.27 ha against 11.87 ha) with a higher proportion of overlapping (11.87% against 0%). Predictions on group size and composition are not confirmed as the difference in mean group size is not statistically significant and as many males per group are found in both habitats (one) but sex ratios (M:F) indicate the presence of more females in Monkey River (1:1.6 against 1:1.3). Also, more infants per group are found in RCNR (0.6 in Monkey River against 1 in RCNR). Those results are likely to be associated with different stage of population growth between the two habitats and more precisely of the hurricane Iris that have lowered the population in Monkey River and allowed more dispersal opportunities and, resulting effects of social factors such as infanticide. Nevertheless, our results indicate howler population to increase again in this disturbed forest. Howlers in RCNR have a more diverse diet (18 food sources in Monkey River against 23 in RCNR) which is likely to be due to higher diversity of plants present in the limestone karst hills. Diets in both habitats differ as only 19.5% of species are similar and species composition in both habitats are pretty different too, which confirms howlers having a flexible diet and being able to adapt their diet to the species found in the habitat. Both populations feed preferentially on leaves but howlers in the secondary forest spent more time feeding on fruits (20.46%) and less on flowers (6.46%) than in the primary forest (11% and 11.75% respectively), although those differences are not significant. Howlers in Monkey River are more active and travel significantly more (9.45% against 5.45%) which is likely to be due to the higher amount of fruits in the diet. Less time is spent in social interactions in Monkey River, which is likely to be due to the smaller number of infants per group. Finally, monkeys in the secondary forest spent significantly more time vocalizing than in the primary forest, which is likely to be due to the higher population density and level of overlap between neighboring groups. No overlap has been recorded in the limestone karst hills and percentage of vocalization is quite low.

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1. INTRODUCTION

1.1. Subject of the Study

This study is about the ecology of black howler monkeys (*Alouatta pigra*). It is done through a comparative approach that allows us to highlight the differences between two populations of howler monkeys living in different habitats. We focus our comparison on food availability, diet, population density, group size and composition, home range size, and activity budget.

1.2. Howler Monkeys: General Comments and Context of the Study

1.2.1 Howlers diversity and ranging

The genus *Alouatta* includes different species listed as *A. belzebul*, *A. caraya*, *A. fusca*, *A. coibensis*, *A. guariba*, *A. nigerrima*, *A. palliata*, *A. sara*, *A. seniculus*, and *A. pigra* according to Groves (2001) and Rowe (1996) and found from Southern Mexico to Southern America. Howler monkeys are thus widely spread in the New World and among the most studied genus within the non-human primates (Di Fiore & Campbell, 2007). However, most of the work has been done on two species: *A. palliata* (e.g., Chivers, 1969; Milton *et al*., 1980; Jones, 1985; Glander, 1992; Zucker *et al*. 1997; Clarke *et al*., 1998) and *A. seniculus* (e.g., Neville, 1972; Sekulic, 1981, 1983; Crockett & Sekulic, 1984; Pope, 1990, 2000). *A. pigra*, commonly called black howler monkeys, are then restricted to the southern Yucatan peninsula of Mexico, western Guatemala and Belize.

1.2.2 Diet

The diet of howler monkeys is mainly composed of leaves, fruits, flowers, stem and seeds. They appear to be mainly folivorous as leaves, an abundant food resource, represent the majority of their diet, with a consumption reaching 45% (*A. pigra*: Silver *et al*., 1998), 58.62% (*A. pigra* Pavelka & Knopff, 2004), 54% (*A.seniculus*: Juliot & Sabatier, 1993), 46,6% (*A. belzebul*: Pinto *et al*., 2003), 82% (*A. caraya*: Prattes & Bitta-marques, 2008). Also, fruit represent an important part of their diet with consumptions generally varying between 25 and 35% depending on the species, and reaching up to 41% for *A. pigra* (Pavelka & Knopff, 2004) which is the most frugivorous species. In some seasons, the diet of *A. pigra* can include up to 67% fruit, making them highly reliant on fruit during months of high productivity (from April to July) (Pavelka & Knopff, 2004). Black howlers are thus considered to be "as folivorous as necessary and as frugivorous as possible" (Silver *et al.*, 1998), consuming fruits preferentially depending on their availability (Pavelka & Knopff, 2004). Finally, flowers, seed and stems are consumed at a minimal level. This capacity to forage on a diversity of food sources indicates the diet of howlers is quite flexible (Cristobal-Azkarate & Arroyo-Rodriguez, 2007; Silver *et al.*, 1998).

1.2.3. Activity budget

Inactive is the most commonly seen behavior in all species of the genus, followed generally by feeding (excepting in a study of *A. belzebul*), travelling and rare social interactions such as playing and grooming. Table 1 presents an overview of the distributions of behavioral activities among different studies and species.

Table 1. Distributions of behavioral activities among different studies on howler monkeys.

Study	Species	Behavioral activity (%)			
		Inactive	**Feed**	**Travel**	**Social**
Cristóbal-Azkárate & Arroyo-Rodríguez, 2007	*A.palliata*	63	24	9	-
Dunn *et al*., 2009	*A.palliata*	68.2	17.7	10.2	-
		53.7	27.7	14.9	-
Pinto *et al*., 2003	*A.belzebul*	53.6	21.6	28.7	0.8
		48.7	15.9	29.3	1.2
Prattes & Bicca Marques, 2008	*A.caraya*	56	-	-	-
Pavelka & Knopff, 2004	*A.pigra*	66.33	18.57	7.49	3.67

It has been long thought that howlers, being the most folivorous of the new world primates (Eisenberg *et al*., 1972) and thus having a low quality diet, behaved according to a characteristic low-energy strategy (Horwich *et al*., 1993). This is well explained by the fact that leaves are energetically poor and difficult to digest forcing folivores to consume them in high quantities and to spend long periods of fermentative digestion (Milton & McBee, 1983). A highly folivorous diet affecting energy expenditure is well illustrated by the black-and-white Colobus (*Colobus polykomos*) (Da Silva, 1992), however, Pavelka and Knopff (2004) have demonstrated that even during periods of high consumption of fruits, black howler monkeys maintained high a level of inactivity, calling into question the causes of this energy minimizing lifestyle. Time spent traveling seems directly affected by the availability in food in the habitat and by the size of the home range in which monkeys have to travel. Indeed, a study on *A. palliata* shows that the shortest daily range was recorded during period of high fruit abundance (Palacios & Rodrigues, 2001) and the authors suggest that the abundance of fruits available allow the monkeys to meet their nutritional needs over a smaller area and allow them to travel less. This increase in time traveling with an increase in fragment size has been found for the same species in three forest fragments in Mexico (Juan *et al*. 2000). Also, Dunn (2009) and Juan *et al*., (2000) found a positive correlation with between the number of species in the diet and time spent traveling. This is explained by the fact that monkeys have to travel more to get to different tree species.

Social interactions are very rare in the genus *Alouatta* in general (Cristobal-Azkarate, 2004), which is thought to be the consequence of the energy-minimizing lifestyle of howlers and the lack of relatives in same social groups. Time spent in social interactions appears to be affected by other predominant activities such as traveling and inactivity. A comparative study shows that groups of *A. pigra* spending more time travelling had less time to devote to social interactions such as playing and grooming (Pavelka & Knopff, 2004). According to Baldwin and Baldwin (1978), infants and juveniles are the age classes that spend the highest amount of time in social playing. This is well illustrated by the drop in social interactions among black

howlers seen after a hurricane caused a decrease in the number infants in the population (Behie & Pavelka, 2005).

Another behavior for which howlers are famous is their long call vocalizations. The function of such vocalizations is generally thought to be agonistic displays informing other groups about their respective location rather than a defined territory (Gavazzi *et al.*, 2008). This allows them to regulate their distances (Carpenter, 1934; Chivers, 1969; Whitehead, 1987) and therefore to minimize the probabilities of potentially aggressive encounters (Whitehead, 1987, 1995). Indeed, Gavazzi *et al.* (2008) observed more vocal confrontation around locations that were visited by several troops and Ostro *et al.* (1999) noted higher level of intergroup aggressions in habitat with relatively high population density, suggesting that howlers defend their current group space and especially when other groups are around.

1.2.4. Habitat and home range

The flexibility of howler's diet seems to allow them to survive in a variety of different habitats. Indeed, howlers can be found in intensive cultivated land (Muñoz *et al*, 2006), mangrove swamp forests, primary and secondary forests, tropical rain forest, and evergreen, semi-deciduous and deciduous forests (Estrada, *et al*. 2005, 2006). Moreover, those monkeys live in fragmented (eg: Pozo-Montuy & Serio Silva, 2006; Zunino *et al.*, 2007; Arroyo-Rodriguez & Dias, 2009) as well as in continuous habitats (eg: Palacios & Rodriguez, 2001; Gonzalez-Kirchner, 1998; Coelho et al., 1976; Schlichte, 1978). In general, their home range size is comprised between 8 to 21 ha for *A.pigra* (Ostro *et al.*, 1999; Gavazzi *et al*., 2008) or between 4 to 67 ha for *A. seniculus* (Sekulic, 1982; Stevenson *et al.*, 1991). This wide variation of home range size likely depends on ecological factors characterizing the habitat such as food availability and population density. According to Dunbar (1987) and Chapman (1988a, 1988b), groups of monkeys living in habitat with lower food availability would need larger home ranges to answer their nutritional needs. For example, the population of *A. seniculus* studied by Palacios & Rodriguez (2001) shows a huge home range of 185 ha probably resulting from "the poor quality of the soil and the consequent diminished productivity of the forest". Also, in their study on reintroduced *A. pigra* in Belize, Ostro *et al.* (1999) showed that a low diversity and abundance of food contributed to the increase in home range size. Indeed, it is generally thought that habitat and vegetation attributes such as abundance, diversity and basal area of top food resources are related to the presence and abundance of primates (Estrada & Coates-Estrada 1996, Cristobal-Azkarate *et al.* 2005). Thus, food abundance has an effect on home range size and primate abundance which in turn can affect home range size (Crockett & Eisenberg, 1987). Indeed, indirect evidences show that when howler population density increases, home range size decreases and degree of overlap increases (Baldwin & Baldwin, 1972; Chivers, 1969; Crockett & Eisenberg, 1987). In a study at Lamanai, were *A. pigra* population density is very high, Gavazzi *et al.* (2008) recorded a 52% mean and up to 63% of overlapping between home ranges.

1.2.5. Population density

Ostro *et al*. (1999) showed that population density was inversely correlated to home range size for *A.pigra* with higher population density in smaller home ranges. Other studies show that high densities of monkeys force groups to diminish their home ranges area due to the presence of competing neighboring groups (Dunbar, 1987; Dobson & Lyles, 1989). Inversely, very large home ranges such as notified previously for *A. seniculus* could also be found in conditions of the very low population density (4ind./km² (Palacios, 1997)) that allow the monkeys to use much larger area (Palacios & Rodriguez, 2001).

1.2.6 .Group size and composition

Social groups in the genus *Alouatta* generally include between 6 to 11 individuals for *A. seniculus* (Chapman & Balcomb, 1998), 6 to 18 individuals for *A. caraya (*Aguiar *et al.* 2009), and 6 to 23 individuals for *A. palliata* (Chapman & Balcomb, 1998). The species *A. pigra* is known to have the smallest social groups with 4 to 7 individuals (Chapman & Balcomb, 1998). Variations in group size between and within species have been documented for primate in general (Clutton-Brock & Harvey, 1977; Dunbar, 1988) but also for *A. pigra* and especially for different populations living in extensive and fragmented forests (Van Belle & Estrada, 2005). Such variations are generally attributed to the variation in ecological factors such as predation pressure or competition for food resources. For instance, a higher predation pressure would select for larger groups (Cheney & Wrangham, 1987; Hamilton, 1971) and inversely, marked competition for limited food resources would select for smaller groups (Chapman & Chapman, 2000; van Schaik, 1989). However, a study on *A. pigra* in Monkey River (Belize) did not find any correlation between mean group size and level of competition for food (Knopff & Pavelka, 2006) suggesting other factors related to the relatively small group size found in black howler monkeys. It is also generally accepted that population density is correlated with mean group size as more monkeys are found in groups living at high population density in *A. palliata* and *A. seniculus* (Crockett & Eisenberg, 1987) and *A. pigra* (Horwich *et al*., 2001; Pavelka *et al*., 2007).

Group composition can be measured according to different ratios. The most commonly used is the sex ratio, defining the mean number of adult males per adult female in a group. Sex ratio shows great variability between different species of the genus as heterosexual pairs, unimale-multifemal groups and multimale-multifemale groups have been observed in *A. palliata*, *A. seniculus*, *A. caraya* and *A. pigra* (Thorington *et al.*, 1984; Crockett, 1985; Rumiz, 1990; Ostro *et al.*, 2001). Such variations can be partly attributed to variations in population density as significant increases in the number of adult females and males in groups with an increase in population density have been recorded (*A. palliata* and *A. seniculus*: Crockett & Eisenberg, 1987; *A. pigra*: Ostro *et al*., 2001). Also Pavelka *et al.* (2007) found a relationship between population density, group size and multimale groups for *A. pigra*. Inversely, after a translocation of groups of *A. pigra* from a forest with high population density condition to a forest with low population density condition, all multimale groups became unimale groups and the number of adult female per group did not exceed 2 (Ostro *et al.*, 2001). The authors concluded that at low population density condition, it was more beneficial for males living in multimale groups to establish new home ranges and form

unimale groups rather than staying in a multimale group. For the same species, Jones (2008) found that groups were larger and more often of the type multimale at higher than at lower population density. Also, for *A. palliata*, Ryan *et al*. (2008) found that larger groups had more male-biased sex ratios.

The relative abundance of females and males in a group seems to be correlated with female reproductive success and survival of immatures. The number of infants in a group is indeed subject to variations among the genus *Alouatta* (Treves, 2001). More females in a group are known to attract more extragroup invasive males (Van Belle & Estrada, 2008) that are potentially infanticide (Crockett & Janson, 2000; van Schaik & Janson, 2000). Inversely, more males in a group are thought to represent a better protection for females against invading infanticide males (Treves, 2001; Van Belle & Estrada, 2008) and contribute to an increase in female's reproductive success (Ryan *et al*., 2008; Van Belle & Estrada, 2008). Thus groups with more males than females would know higher survival of infants.

1.2.7. Context of the study

Knowing that howler monkeys show intraspecific variations in population density (Ostro *et al.*, 2001; Van Belle & Estrada, 2005), group size and composition (Ostro *et al.*, 2001; Van Belle & Estrada, 2005), ranging behavior (Ostro *et al*., 1999, 2000, Arrowood *et al.*, 2003), feeding behavior (Silver *et al.*, 1998), vocalizations patterns (Cornick & Markowitz 2002), and home range size (Cristobal-Azkarate & Arroyo-Rodriguez, 2007) across different habitat type, it would be interesting to drive a comparison of the variables discussed above known to be inter-correlated. To date, only three comparative studies have been done on *A. pigra*; Ostro *et al*. (1999, 2000) compared the ranging behavior of monkeys living in different types of secondary forests (Community Baboon Sanctuary) with those of monkeys translocated from that same forest to semi-evergreen and evergreen broadleaf tropical forests (Cockscomb Bassin Wildlife Sanctuary). Jones (2008) compared the effect of the forest type (riparian Vs deciduous) on male residence. Finally, Gavazzi *et al.* (2008) although they did not actually compare two sites, introduced the effect of forest type and food abundance on ranging behavior of black howlers. Moreover, most studies on *A. pigra* have been done in fragmented habitats (Van Belle & Estrada, 2005). To date, only three studies have been conducted on *A. pigra* inhabiting extensive undisturbed forest: two focused on group size and population density in Mexico (Muchukux forest (Gonzalez-Kirchner, 1998)), another in Guatemala (Tikal National Park (Coelho *et al*., 1976; Schlichte, 1978)) and a third one focused on population density, group size and age-sex ratio of 8 populations across Mexico and Guatemala (Van Belle & Estrada, 2005).

1.3. Study habitats

1.3.1. Monkey River

Monkey River is 52 ha site in southern Belize in a lowland semi-evergreen riparian forest in a subtropical moist life zone. The topography of this forest is more or less flat. The

average temperature is 26°C and the average rainfall is 4064mm (Belize Government, 2010). This site is part of a 96-km² forest fragment bordered on the north and south by coastal plain savanna, on the east by the Caribbean Sea and on the west by the Southern Highway and human settlements including agricultural fields.

Figure 1. Aerial picture of the Monkey River study area.

Only one species of monkey, the black howler monkey (*Alouatta pigra*) is found at this site. Eight social groups have been closely monitored in the site from 1998 to 2001 when hurricane Iris struck the Belizean coastline, and the study site that was directly on its path. This category four hurricane (on a scale of five) caused massive damage to the ecosystem. The data collected the months following the hurricane showed that the monkey population has been reduced by 42% (Pavelka *et al*., 2003). A later study in 2004 showed a loss of population of 88% in the entire forest fragment (Pavelka *et al*., 2007). Indeed, the population continued to decline over the 29 months following the storm which can be partly explained by the decline in food availability (Pavelka & Chapman, 2005). Iris caused the complete loss of the canopy and the complete defoliation of the trees (Pavelka *et al*. 2003). According to data collected in 2002, 35% of the howlers food trees have been lost found following the hurricane. This constrained the howlers to feed on 14 species after the hurricane compared to 28 before, thus causing a heavier reliance on fewer species (Pavelka & Behie, 2005) and on a more folivorous diet as little fruit was available in the forest. Also, Geographic Information System (GIS) analyses of satellite data showed that the hurricane increased the amount of edge habitat, decreased patch size, and increased the number and isolation of patches within the study site (Alexander *et al.* 2006). Because of the cumulative effects of the hurricane and the human settlements around, this forest is therefore considered at secondary stage. However, it is important to consider that the data available have been collected within a year after the hurricane and that the data for this study have been collected more than 6 years after. This time must have allowed a minimum recovery of plants and monkey population and allow us to reconsider the monkey population and the food trees in this recovering forest.

1.3.2. Runaway Creek Nature Reserve (RCNR)

Runaway Creek is a private reserve located in central Belize. The average rain fall is 2000-2200 mm (Meerman, 1999). This reserve encompasses 2432 hectares and represents an important biological corridor between two of the largest remaining forest blocks in the country. There are a variety of different vegetation types found at RCNR including marshlands, pine savannah, riparian forest, limestone ridges, and tropical forests. A REA (Rapid Ecological Assessment) made by Meerman (1999), describes the vegetation in the forest as tall semi-evergreen or evergreen forest. Also the topography in RCNR consists of elevated karst limestone hills. Such limestone formations are considerably porous and characterized by great variations in their topography and by steep and irregular ground surfaces (Crowther, 1982). There is also a considerable level of drainage of nutrients (Furley & Newey, 1979) and runoff from upper to lower areas. Such patterns have been found in Belizean (Furley & Newey, 1979) and Malaysian karst hills. Indeed, lower areas in Belizean karst hills are proven to have more nutrients and moisture than upper area resulting in more potential for plant growth (Furley & Newey, 1979). Thereby, it appears that ecological conditions are not homogeneous in this forest and Meerman (1999) recorded a wide diversity of vegetation patterns. The tropical forest is relatively undisturbed as human impact on the reserve as well as on its periphery is minimal. The only known harmful effects are occasional poachers coming in the reserve and the proximity of the unpaved western highway. There are

two species of monkeys in RCNR: black howlers monkeys (*A. pigra*) and black handed spider monkeys (*Ateles geoffroyi*).

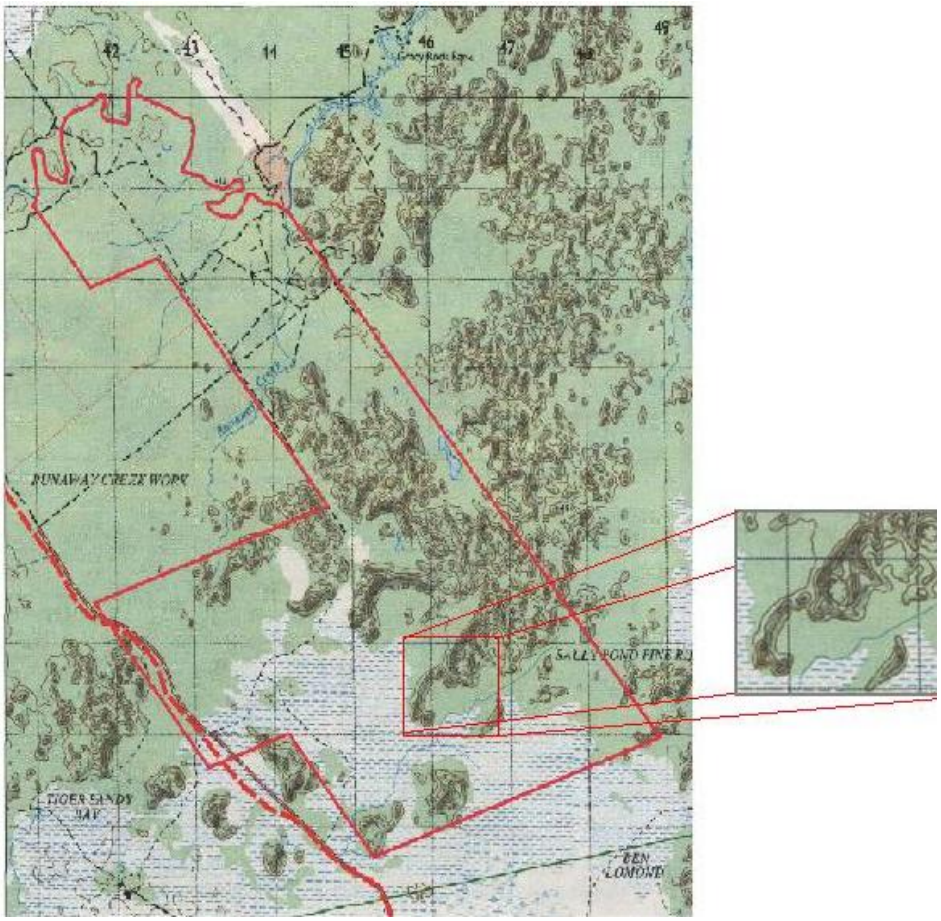

Figure 2. Topographic map of the Runaway Creek Nature Reserve and location of the study area.

An important characteristic of this ecosystem is the presence of those two primates species living sympatrically. The presence of *Ateles geoffroyi* in RCNR indicates it is probably an undisturbed habitat as spider monkeys are very sensitive to habitat disturbance and rely on ripe fruits and need large home ranges (Di Fiore & Campbell, 2007). Spider monkeys are primarily frugivorous (Chapman, 1990) but also eat new leaves and could represent therefore a competing species with howler monkeys that also feed on fruits and new leaves. As a result of this sympatry, one could expect indirect competition to force both species to forage over a greater area because of reduced foraging efficiency per patch (Terborgh & Janson, 1986). To a greater extent we can expect this sympatry to limit the howler monkey population as food abundance (Milton, 1980, 1982; Froehlich *et al*., 1981; Crockett, 1985) and the number of competing primate species (Struhsaker, 1978; Eisenberg, 1979; Crockett, 1985) have traditionally been thought to limit primate density and thereby to influence the structure of populations (Chapman & Balcomb, 1998). Also, the occurrence of direct competition through aggressive interactions between spider and howler monkeys have been previously recorded (Simmen, 1992; De Gusta & Milton 1998). Such competitions could

drive a species to avoid encounters with the other competing species which can in turns affect its ranging behavior in the habitat.

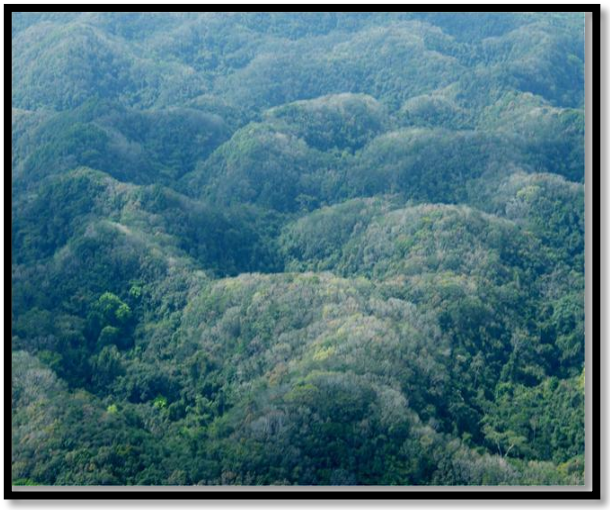

Figure 3. Aerial view of the rain forest and limestone karst hills in RCNR.

1.4 Objectives and Interests of the Study

The present study gives rise to two mains objectives. The first objective of this study is to report on the ecology of black howler monkeys in RCNR which is a previously unstudied population that live in a relatively undisturbed karst limestone hill ecosystem. To date there have been no howler monkeys studied in this type of ecosystem. This will allow us to report population parameters such as population density, age-sex ratio and group-size for a previously unstudied population of *A. pigra* in Belize. The second objective of this study is to compare those parameters as well as the diet, activity budget and ranging patterns with another population of howler monkeys living in Monkey River. RCNR and Monkey River are two habitats presenting different characteristics expected to influence black howler monkeys population parameters (density and structure) and ecology (diet, home range size and activity budget).

1.5. Hypothesis and Predictions

1.5.1 Hypothesis

In the present study we compare two forests that are very different regarding their ecological type, disturbance, annual rainfall, history and other factors that are not measured here. The main variable we use to contrast the two sites is the food availability for black

howler monkeys populations in their respective habitats. Following are hypothesis on how the studied variables should be correlated:

a. Food availability should affect diet.
b. Food availability should affect population density.
c. Food availability should affect home range size.
d. Population density should affect group size and composition.
e. Food availability should affect activity budget.
f. Population density should affect activity budget.

1.5.2 Predictions

Firstly, considering the amount of time elapsed between the hurricane in 2001 and the collection of the data in Monkey River used for this study (2007), we can considerer that if the forest is recovering, the monkey population would be recovering as well, and we should bee able to notice a difference in population parameters. Therefore, we predict that population density and mean group size should be higher in this study than soon after the hurricane.

Two points allow us to predict higher food availability in Monkey River. Firstly, the rain fall is higher in Monkey River and according to Chapman and Balcomb (1998) habitat productivity increases with rain fall. Therefore, primary productivity should be higher in Monkey River, which should translate into a higher abundance of plants (Chapman and Balcomb, 1998; Hall, 1977). Secondly, because of the specific topography and the heterogeneous distribution of nutrients in RCNR, primary productivity should be more homogeneous and higher in Monkey River and we therefore predict to find higher food availability in Monkey River.

As well, because of this higher productivity, more fruits should be available in this forest and we predict howlers in Monkey River to spend more time feeding on fruits and flowers than in RCNR.

Because of the diversity of ecological conditions found in the limestone karst hills (Meerman, 1999), more diverse vegetation patterns should result from it and we predict there to be higher plant species diversity in RCNR.

As a result of this higher diversity of plants, howlers should have more potential food species available and we predict them to have a more diverse diet in RNCR than in Monkey River.

We predict that the higher food availability in Monkey River should allow more howlers to live in this area (higher carrying capacity) (Milton, 1980; Crockett, 1985), resulting in a higher population density in Monkey River than in RCNR.

Regarding group size and composition, the higher population density in Monkey River should force howlers to live in larger groups. We predict therefore mean group size to be higher in Monkey River. We predict also to find more groups of the type multimale-multifemale in Monkey River whereas groups in RCNR should be of the type heterosexual

pairs and unimale-multifemale. We predict therefore to find relatively more males in Monkey River. As the result of this biased sex-ratio, we predict to find more infant in Monkey River.

The higher food availability in Monkey River should allow howlers to meet their nutritional needs over smaller area. Moreover, because of possible scramble competition for food in RCNR with the competing spider monkeys, and the potential resulting decreased food availability, we predict that home ranges in RCNR should be larger than in Monkey River.

Also, because of the higher population density predicted in Monkey River, we predict neighboring home ranges in Monkey River to present higher degree of overlapping.

Because of larger home ranges, lesser food availability and more diverse diet predicted in RCNR, we predict howlers in RCNR to spend more time travelling than in Monkey River. As a result, we predict howlers to be more active in RCNR and, also due to the lower number of infants predicted in RCNR, howlers should spend less time in social interactions.

Finally, because of a higher population density and higher degree of overlapping home ranges in Monkey River, howlers should have a more important need to inform neighboring groups about in their location and we predict thereby howlers in Monkey River to allocate more time to vocalization

2. METHODS

2.1. Study Sites and Groups

2.1.1. Monkey River

During the study in Monkey River a total of 70 hours of focal observation has been collected in the dry season of 2007, from February to May. The data have been collected on 5 howler groups named Q, A, B, N and G. A same group was not observed two days in a row.

2.1.2. RCNR

Within the RCNR, howler monkeys groups have been observed in a portion of the study area as shown in figure 2. During the study period in RNCR a total 76.5 hours of focal observation has been collected during the dry season of 2010, from February to May. The field work took place from Sunday to Thursday from either 6am to 2pm or from 10am to dark. We tried not to observe a same group two days in a row but as groups ranges were not known previous to this study, groups could not be found systematically. The total number of focals and scans and the number of days spent in the field in the morning and in the evening have been balanced between the two groups of study. A total of 3 groups have been found in this area but only 2 of them have been used to collect the data on a regular basis. Those are the groups Hn and Wn. The third group Mn has been found and observed one day but not again later. All of these groups have become used to the consistent presence of humans in the area doing research on spider monkeys since 2007, and are therefore considered to be habituated.

2.2. Data Collection

2.2.1. Vegetation sampling

To calculate plant species diversity in Monkey River, 48 quadrats of 20 meters by 20 meters have been established, representing a total of 1.92 ha of forest that has been sampled. In RCNR, 16 quadrats of 40 meters by 40 meters have been established, representing a total of 2.56 ha of forest that have been sampled.. The same collection protocol was used in both habitats: a measuring tape has been used to measure out all of the sides, each corners have been flagged and marks at half the length of each side have been made on each side. From those, distances of half the length of a side have been measured in order to mark the center of each quadrat, thus separating the quadrat into 4 sections. We then went systematically through each section identifying and measuring trees at breast height that had a DBH (diameter at breast height) of 30cm or more. The locations of the quadrats were randomly selected, but we tried to get a representation of the different habitat types in the area.

2.2.2. Behavioral observations

Behavioral data collection has been conducted using the frequency scan method as described by Struhsaker (1975) and the focal animal sampling as described by Altmann (1974). Scans have been done every 30 minutes and those included the weather, the GPS coordinates of the group being observed, the composition of the group, the spread of the group and the behavior of all individuals within the group. A maximum length of 5 minutes was allowed to record the behavior of all individuals and behavior was not recorded for five seconds after an individual was spotted, in order to remove the bias of recording movement as the behavioural state. Between two scans, focals were conducted, each for a duration of 10 minutes per individual during which all behaviors of the focal animal were recorded. The same individual was not sampled within the next 30 minutes following his last focal sampling. Infants dependant on their mother were not sampled as their behavior is strongly influenced by their mother. The difference between state behaviors and events is made. When the monkeys where observed feeding, the species and plant part being eaten was recorded whenever possible.

2.3. Data Processing and Analysis

All statistical tests were run using the software Statistica 7.0 (StatSoft. Inc). Previous to statistical tests, normal distribution of the variables was tested and in consequence, parametric or non-parametric tests were run. Significant difference were considered at a p-value <0.05.

2.3.1. Diet

The total amount of time spent feeding on each food species have been calculated and the sum of the most commonly eaten food species were calculated to obtain the food species accounting for 80% of the total feeding time.

In order to get the diet composition, plants parts such as new leaves (NL), mature leaves (ML), unknown leaves (UL) and leaf buds (LB) where combined into the category called “leaf” and used to assess the proportion of leafy material in the diet of the monkeys. Then, fruits (Fr) were combined into the category “Fruit” and flowers (Fl) into the category “Flower” and respectively used to assess the proportion of fruits and flowers in the diet. Finally, plant parts such as stem (St) and seeds (Se) were combined into the category “other” but this part was excluded from the statistical analysis as it was rare and so little that it could not account for a significant difference in the diet composition. Feeding behaviors when the plants part where unknown were not considered for the analysis of diet composition but all the food species recorded were used to assess time spent feeding on each diet category. The amount of time monkeys have been observed each day can vary widely and lead to considerable numbers of 0% and 100% of daily time spent in either diet category. This great variance obtained for each habitat does not allow us to highlight eventual statistical differences between times spent eating on each diet category. Therefore, we cumulated daily values into weekly values in order to obtain the weekly proportion of time spent eating on

each category to get more accurate variance for each habitat. Thus, a total of 16 weeks have been used for each habitat as the unit sample for comparison. Then, in order to test for the difference in mean time spent in the category "leaf" an independent t-test have been run whereas for the categories "fruit" and "flower" a Mann-Whitney U-test has been run. Finally, we compare the dietary similarity in the respective habitat of the monkeys using the Sorensen's coefficient (S) as defined by: S=2C/A+B where C is the number of species shared in both habitats and A and B the number of species specific for both habitats (Cristobal-Azkarate & Arroyo-Rodriguez, 2007). When different species could not be specified, they were included into a food source category which was considered as one species for this analysis. This is to avoid an observation bias, as species included in a food source were differentiated in one habitat (such as vines in RCNR) but not in the other.

2.3.2. Food availability

Food availability is defined as the amount of food available for the monkeys in their habitat. The amount of food available is based on the diet composition recorded in respective habitats. It is measured by the proportion of total basal area of food tree species relative to the total basal area of all trees sampled in the quadrats. According to Chapman *et al*. (1992), DBH (diameters at breast height) is directly related to the basal area of the trunk and provides the best estimates of fruit abundance in trees. As a result, basal area is used to measure fruit and leaf abundance in the present study. Then, higher the percentage of relative basal area is, higher the food availability is in a given area. The food species accounting for 80% of the total feeding time, as well as all the food species were considered to compare food availability. Species diversity present in each habitat was calculated and the similarity of species present in both habitats was tested using the Sorensen's coefficient (S). The vines and epiphytes (Philodendron) were not considered in the quadrats so they were not included in the calculation of food availability.

2.3.3. Population density

We express population density (individuals/km^2) in terms of number of individuals present in the area sampled during the study periods. Thus, numerators include all individuals studied in social groups as well as spotted solitary individuals. Denominators are not home range sizes of the observed social groups but total areas including areas between observed home ranges that have been checked for presence of howlers on a regular basis. Those were plotted using GPS coordinates collected in the field and calculated using the GIS software Arc View.

2.3.4 Groups size and composition

Group size is defined here by the total number of individuals within a social group, including infants. Group composition is defined by the sex ratio, so by the number of males per female. We also look at the mean number of infants per group.

A Mann-Whitney U-test has been run to test for the difference in group size between the two habitats.

2.3.5. Home range

GPS coordinates of observed social groups have been recorded every 30 minutes over entire study periods. Then, home ranges have been plotted using the minimum convex polygon technique thanks to the GIS software Arc View. Percentage of overlapping was calculated as the ratio of the surface area in which different social groups have been sighted to the surface area in which one given social group have been sighted (Gavazzi *et al*., 2008)

A Mann-Whitney U-test has been run to test for the difference in home range size between the two habitats.

2.3.6. Activity budget

For the analysis, behaviors were categorized into five different categories: inactive (includes resting, sitting in body contact, sitting near another individual and scanning), travel (includes locomote and travel), feed, social (includes grooming and social play behavior) and vocalization (including only long distance vocalizations and not quick vocalizations). In order to test for the difference in mean time allocated to each behavioral activity between the two habitats, Mann-Whitney U-tests have been run.

3. RESULTS

3.1. Food Availability

In Monkey River, the total basal area of the food tree species accounting for 80% of the diet represents 25.48% of the total basal area of the trees present in the habitat (table 2). When taking into account all food species that have been sampled, this habitat has a food availability of 40.14% resulting in an increase of 14.66% when all food species are included

In RCNR, the total basal area of the food tree species accounting for 80% of the diet represents 19.7% of the total basal area of the trees present in the habitat (table 3). While taking into account all food species sampled, this habitat has a food availability of 27.91%, resulting in an increase of 8.2% when all the food species are included. However, it appeared that one species (Chaparro) in Monkey River and three species (Swamp Kaway, Welliam, and Copna) in RCNR were not found in the quadrats and were not therefore included in the total basal area of food trees.

Table 2. Relative basal area (%) of howler's food species in Monkey River relative to the total basal area of all the tree sampled.

Common name	Relative basal area (%)
Black Bay Ceddar[a]	6.24
Breadfruit	0.55
Cabbage Bark[a]	0.28
Chaparo[c]	-
Cochito	0.05
Fiddle Wood[a]	0.78
Fig[a]	0.47
Freshwater Moho	0.08
Hogplum	3.68
Inga	0.71
Swamp Kaway[a]	0.23
Prickly Yellow	0.23
Provision	1.03
Royal Palm[a]	1.94
Sering	0.21
Strangler fig[a]	1.21
Trumpet[a]	1.20
Vines[ab]	-
Yellow Bay Cedar	8.11
Total[a]	**25.48**
Total	**40.14**

[a] Species accounting for 80% of the diet.

[b] Non-tree growth form that was not included in the quadrats

[c] Species that have been observed to be part of diet but not found in the quadrats.

Table 3. Relative basal area (%) of food species of howlers diet in RCNR compare to the total basal area of all the tree sampled.

Common name	Relative basal area (%)
Acacia[a]	0.82
Ball Seed tree	0.20
Copal[a]	2.18
Copna[c]	-
Cream wood	0.22
Fiddle Wood	5.91
Fig[a]	2.96
Jobillo	1.68
Iron wood[a]	1.21
Swamp Kaway[c]	-
Mammee Cirella	0.42
Negrito[a]	1.30
Philodendron[b]	-
Rain tree[a]	1.24
Red Gumbolimbo	0.89
Red Ramon	0.70
Red sillion	0.36
Tamatama bribri	0.19
Vines[ab]	-
Warrie wood	4.74
Welliam[c]	-
Wild Breadnut[a]	1.79
Wild Cherry[a]	1.10
Total[a]	**19.70**
Total	**27.91**

[a] Species accounting for 80% of the diet.

[b] Non-tree growth form that was not included in the quadrats

[c] Species that have been observed to be part of diet but not found in the quadrats.

3.2. Diet

3.2.1. Food species in Monkey River

Howler monkeys diet in Monkey River is composed of 20 food sources, including different unspecified species of vines included into the category "Vines" (table 4). At least one species of fig (Strangler Fig) have been differentiated here but not in RCNR then, in order to compare more accurately with the diet in RCNR, we can include this species into the category "Fig". At least one species of vine (Catclaw) have been differentiated here but it is included into the category "Vines". Thus we consider 18 different food sources for this habitat. Eight different food sources account for about 80% of their diet (table 5). Of those 80%, three food sources are shared with the other habitat (Swamp Kaway, Fig and Vines), which are by the way the only food sources shared between the two habitats within their whole diet.

Table 4. Common and scientific names and families of food plant species accounting for the diet of *A. pigra* in Monkey River, Belize.

Common name	Family	Genus and species name
Black Bay Cedar	Anacardiaceae	*Guazuma ulmfolia*
Breadfruits	-	-
Cabbage bark	Fabaceae	*Andira enermis*
Catclaw	-	*Uncaria tomentosa* -
Chaparro	-	*Curatella americana*
Cochito	Myrtaceae	*Myriciara floribunda*
Fiddle wood*	Verbenaceae	*Vitex gaumeri*
Fig*[a]	Moraceae	*Ficus spp*
Freshwater Moho	-	-
Hog Plum	Anacardiaceae	Spondias mombin
Inga	Fabaceae	*Inga edulis*
Swamp Kaway*	Fabaceae	*Pterocarpus officinalis*
Prickly Yellow	Rutaceae	*Zanthoxylum kellermanii*
Provision	Bombaceae	*Pachira aquatica*
Royal Palm	Arecaeae	*Roystonia regia*
Sering	Melastomaceae	*Miconia argentea*
Strangler Fig	Moraceae	*Ficus crassiuscula*
Trumpet tree	Moraceae	Cecropia obtusifolia
Vines* [a]	-	-
Yellow Bay Cedar	Malvaceae	*Luehea seemannii*

* Food sources that are shared in the two habitats.

[a] Unspecified food source that may includes different species.

Table 5. Percentage of time eaten and plant part eaten of food species in Monkey River, Belize.

Genus and species name	Frequency (%)		Plant part eaten
Swamp Kaway*	15.12		LB, NL, ML
Vines*[a]	14.80		NL, ML
Trumpet	13.70		Fr, LB, NL, ML, St
Cabbage bark	10.48	≈80%	NL, LB
Fig*[a]	10.11		Fr, LB, NL, ML, St
Black Bay Ceddar	8.11		Fr
Fiddle wood	4.29		NL, LB
Royal Palm	3.97		Fr
Cochito	3.27		Fr
Breadfruit	1.34		ML, LB
Sering	1.20		Fr
Hogplum	0.97		Fl, NL
Chaparo	0.92		Fr, ML
Inga	0.78		NL, ML
Freshwater Moho	0.35		Fl
Provision	0.30		NL
Prickly Yellow	0.24		NL
Yellow Bay Cedar	0.23		Fl
Unknown	9.82		-

*Food sources that are shared in the two habitats.

[a] Unspecified food source that may includes different species.

3.2.2 Food species in RCNR

The diet in RCNR it composed of a total of 26 food plants, including different unspecified species of fig included into the category "Fig" (table 6). Four different species of vines (Blood vine, Sapintaceae vine, Sandpaper vine and Snake vine) have been here differentiated, then, in order to compare more accurately with the diet in Monkey River, we can include those four species into the category "Vines". Thus we consider a total of 23 food sources in this habitat. In RCNR, nine food sources account for about 80% of the diet (table 7) which is more than in Monkey River. Among those, only two food sources (Fig and Vines) are shared with the diet in Monkey River. Swamp Kaway which is the most commonly eaten species in Monkey River and account for 15.12% of the total feeding time accounts for only 1.59% of the total feeding time in RCNR.

Table 6. Common and scientific names of food plant species accounting for the diet of *A.pigra* in RCNR, Belize.

Common name	Family	Genus and species name
Acacia	Fabaceae/Mimosoideae	*Acacia dolichostachya*
Ball Seed tree	Fabaceae	*Andira enermis*
Blood vine	Maecherium	-
Sapindaceae vine	Sapindaceae	-
Copal	Burseraceae	*Protium copal*
Copna	-	*Erythrina*
Cream wood[b]	Sapotaceae	*Sideroxylon floribundum*
Fiddle wood	Verbenaceae	*Vitex gaumeri*
Fig*[a]	Moraceae	*Ficus spp*
Jobillo	Anacardiaceae	*Astroneum graveolens*
Iron wood	Fabaceae/Caesalpinoideae	*Dialium guianense*
Swamp Kaway*	Fabaceae	*Pterocarpus officinalis*
Mammee Cirella[b]	Sapotaceae	*Pouteria dourlendii*
Negrito	Simaroubaceae	*Simarouba glauca*
Philodendron[b]	Araliaceae	-
Rain tree	Fabaceae/Mimosoideae	*Samanea saman*
Red Gumbolimbo	Burseraceae	*Bursera simaruba*
Red Ramon	Moraceae	*Trophis racemosa*
Red sillion[b]	Sapotaceae	*Pouteria amygdalina*
Sand paper vine	-	-
Snake vine	-	-
Tamatama bribri	Fabaceae/Mimosoideae	*Inga edulis*
Warrie wood[b]	Fabaceae	*Caesalpinia gaumeri*
Welliam[b]	-	-
Wild Breadnut	Moraceae	*Brosimum alicastrum*
Wild Cherry	Moraceae	*Pseudomeldia spuria*

* Food sources that are shared in the two habitats.

[a] Unspecified food source that may includes different species.

[b] Species that have been observed to be briefly consumed during the study period but not recorded into the feeding behavior for use in the analysis.

Table 7. Frequencies as percentage of the diet and plant part eaten of food plant species accounting for the diet of *A.pigra* in RCNR.

Genus and species name	Percentage in the diet		Plant part eaten
Fig*	28.92		Fr, NL, St
Vines*	20.43		Fl, LB, NL, St
Copal	8.90		NL
Negrito	4.88		Fr, NL
Wild Breadnut	4.72	≈80%	Fl, Fr, NL
Iron Wood	3.56		Fr, NL
Acacia	3.42		Fl, NL
Rain tree	2.23		NL, ML
Wild Cherry	2.19		Fr, Fl
Tamatama bribri	1.99		Fl, UL
Red Ramon	1.79		NL
Red Gumbolimbo	1.61		NL
Swamp Kaway*	1.59		LB, NL
Gobillo	1.49		NL
Bastard Rose	1.14		NL
Fiddle wood*	0.89		NL
Ballseed tree	0.68		NL
Copna	0.58		Fl, Fr, NL
RoyalPalm	0.43		NL
Philodendron[b]	-		-
Red sillion[b]	-		-
Warrie wood[b]	-		-
Welliam[b]	-		-
Unknown	8.39		-

* Food sources that are shared in the two habitats.

[b] Species that have been observed to be briefly consumed during the study period but not recorded into the feeding behavior for use in the analysis.

3.2.3. Similarity in habitats and diets

According to the quadrats made in both habitats, 42 species of plants have been identified in Monkey River and 90 in RCNR, 18 of them are shared between the two habitats. Thus, with Sorensen's index of similarity, it appears that 27.3% of plants species are shared between the two habitats.

Howlers in the two habitats share a total of 4 food sources (Fig, Vines, Swamp Kaway and Fiddle wood). According to the Sorensen's coefficient, those represent 19.5% of their food sources.

3.2.4. Diet composition in Monkey River and RCNR

Diet in Monkey River (figure 4a.) is principally composed of leaves, 72.64%, then of fruits, 20.46%, flowers with 6.46% and other food items with 0.29% of total feeding time. Diet in RCNR (figure 4b.) is also principally composed of leaves with 76.91%, then of fruits with 11%, flowers with 11.75% and other food items with 0.34% of total feeding time. The time spent feeding on leaves between the two habitat is not statistically significant (independent t-test: t=-0.57, p=0.57), neither for fruit (Mann-Withney U-test: U=89.5, p=0.13), nor for flower (Mann-Whitney U-test: U=110.5, p=0.52).

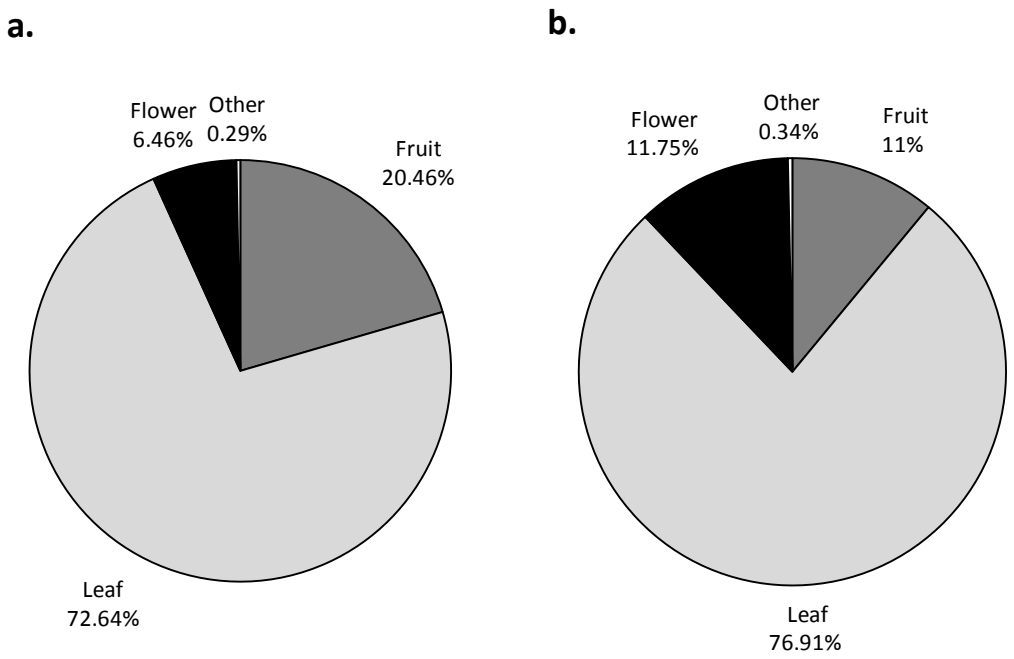

Figure 4. Diet composition of black howler monkeys in Monkey River (a.) and RCNR (b.), Belize.

3.3. Population Density

3.3.1. Variations in population densities in Monkey River

Total area that has been sampled for the calculation of population density in Monkey River in the present study measures 58.35 ha. Table 8 presents different population densities that have been measured at different periods in the study area.

Table 8. Population densities in the Monkey River study area at different periods.

Period	Year	Population density (ind./km²)
Pre-hurricane	1999-2001[1]	101.92
Post hurricane	2002 (Feb)[2]	60
	2002 (May)[2]	56
	2004[1]	23
	2007[3]	44.82

[1] From Pavelka & Chapman, 2005.
[2] From Pavelka *et al*., 2003.
[3] Present study.

3.3.2. Population density in RCNR

Total area that has been sampled for the calculation of population density measures 61.39 ha in RCNR. Population density is 26 individuals/km².

3.4. Group Size and Composition

3.4.1. Variation in mean group size in Monkey River

As we see in table 9, results from different studies show that mean group size in Monkey River was 6.4 before the hurricane, and decreased until 3.7 in 2004. Since then, mean group size seems to have increase to reach 5.2 in 2007.

Table 9. Mean group size in the Monkey River study area at different periods.

Period	Year	Mean group size
Pre-hurricane	1999-2001[1]	6.4
Post hurricane	2002 (Feb)[2]	5.2
	2002 (May)[2]	5
	2004[1]	3.7
	2007[3]	5.2

[1] From Pavelka & Chapman, 2005.
[2] From Pavelka *et al*., 2003.
[3] Present study.

3.4.2. Group size and composition in Monkey River and RCNR

As shown in table 10, mean group size is slightly larger in Monkey River with 5.2 individuals against 5 individuals in RCNR. This difference is not statistically significant (Mann-Whitney U-test: U=7.5, p=1.0). In total there are 8 adult females, 5 adults in Monkey River and 4 adult females and 3 adult males in RCNR. In RCNR there is an average of 1 infant per group whereas in Monkey River there is an average of 0.6 infant per group. Sex ratio (adult males per adult female) is higher in Monkey River (1:1.6) meaning there are more males per females in RCNR (1:1.3).

Table 10. Mean group size and composition for black howler monkeys in Monkey River and RCNR.

Habitat	Mean group size	# Adult F	# Adult M	Mean # infants	Sex ratio (M:F)
Monkey River	5.2	8	5	0.6	1:1.6
RCNR	5	4	3	1	1:1.3

3.5. Home Range

Home ranges in Monkey River are smaller and present more overlapping area than in RCNR. The difference in home range size is not statistically significant (U Man-Whitney test: U=0, p=0.10).

3.5.1. Home ranges in Monkey River

Home ranges for the dry season of 2007 in Monkey River are illustrated in figure 5. Home range size and situation are available only for four groups (N, B, Q , A) as the group G has not been followed enough time to get an home range size estimate that would be proportional with the other groups. Group N, composed of 6 individuals, has a home range of 3.76 ha. Group N is not overlapping with the other groups but it is worth noting a road separates group N from the other groups. Group B, composed of 6 individuals has a home range of 3.43 ha and 11.8% (0.4 ha) of overlapping with the group A. Group Q composed of 4 individuals has a home range of 2.64 ha and 5.3% (0.14 ha) of overlapping with group A. Finally, group A composed of 3 individuals has a home range of 3.05 ha and 17.9% of overlapping (0.4 ha with the group B and 0.4 ha with the group Q). Mean size of home ranges in Monkey River is therefore 3.22 ha and mean overlap is 11.7%.

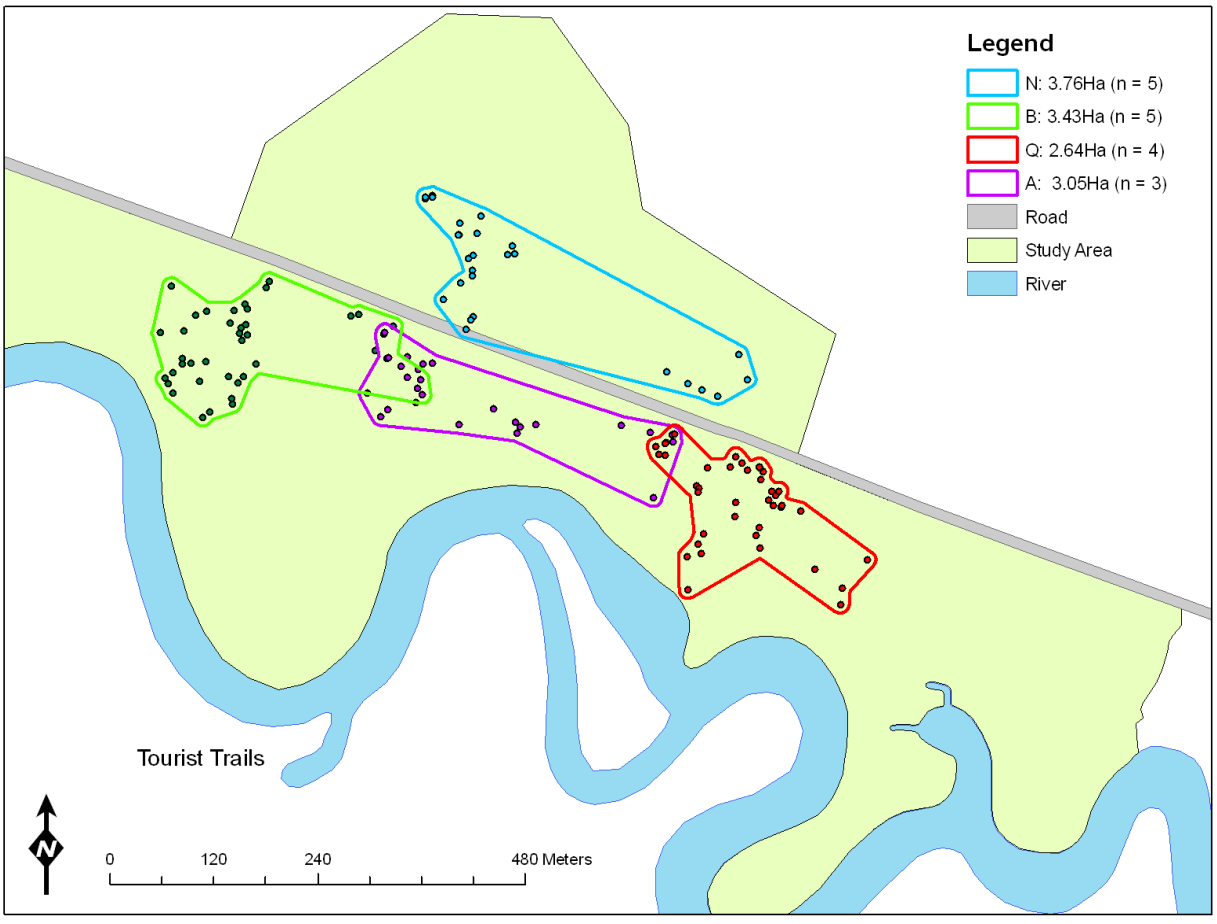

Figure 5. Map of the Monkey River study site illustrating home ranges for howler groups N, B, Q and A

3.5.2. Home ranges in RCNR

Home ranges in RCNR for the dry season of 2010 are as illustrated in figure 6. Group Wn composed of 3 individuals has a home range of 4.61 ha and the group Hn composed of 7 individuals has a home range of 19.13 ha so four times larger than Wn home range. Mean size of home range in RCNR is therefore 11.87 ha. The group Mn have been observed only one day in the area so its home range can not be illustrated. Over the study period, 0% of overlap of home ranges between the neighboring groups Hn and Wn have been recorded and no other howler group have been observed in the area between Hn and Wn home ranges where researchers have been circulating on a daily basis.

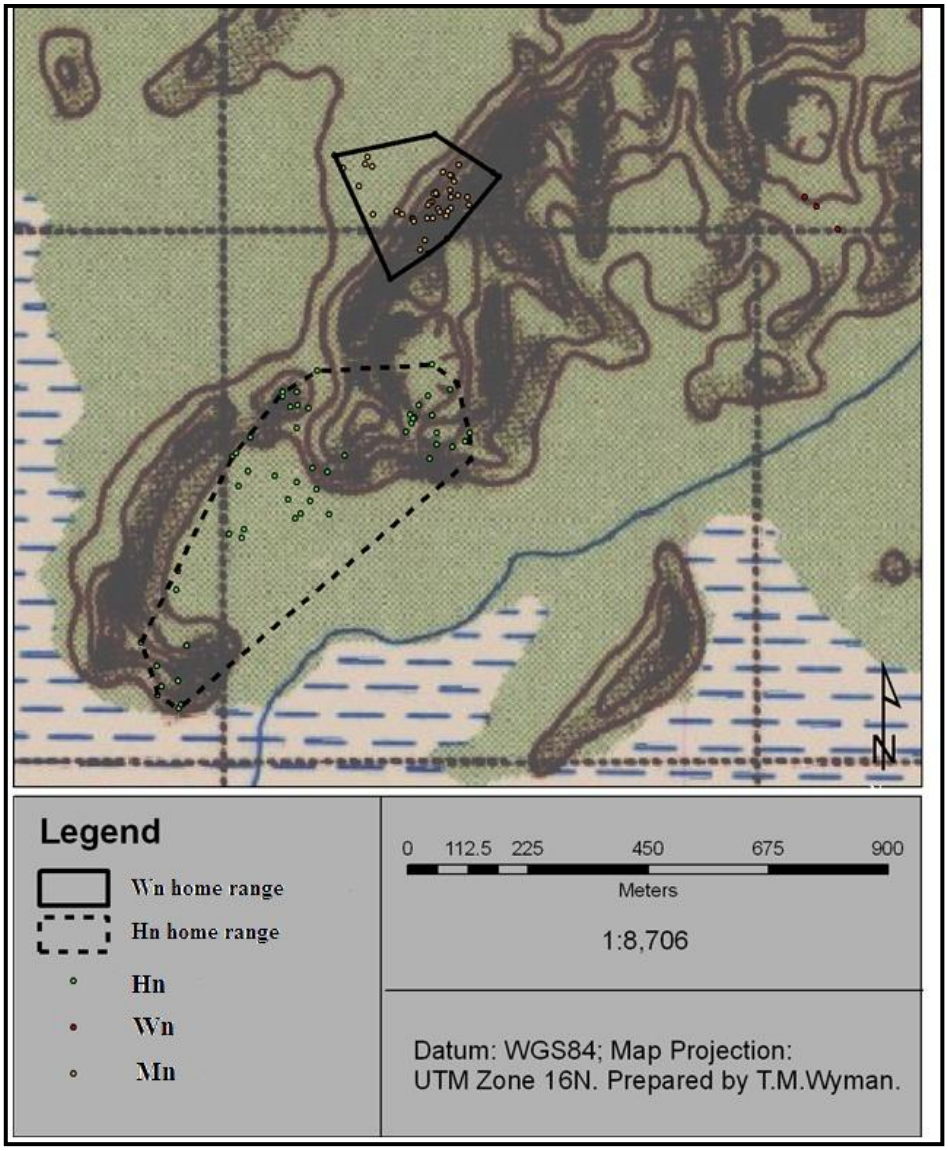

Figure 6. Map of the study area in RCNR with Wn and Hn groups home ranges and location of Mn group.

3.6. Activity Budget

When looking at activity budgets in both habitats (figure 7) it appears that monkeys in Monkey River spend 64.54% of their time inactive, whereas monkeys in RCNR spend 70.84% of their time inactive. This difference is not statistically significant (Mann-Whitney U-test: U=89; p=0.22). Monkeys forage for 22.96% of their time in Monkey River against 21.97% in RCNR, a slight difference which is not statistically significant (Mann-Whitney U-test: U=116, p=0.89). Howlers in Monkey River travel significantly more than those in RCNR with 9.45 and 5.49% respectively (independent t-test: t=2.84, dl=29, p=0.008). Howlers in Monkey River spend 1.14% of their time in social interactions against 1.44% in RCNR, a slight difference which is not significant (Mann-Whitney U-test: U=88, p=0.39). Finally, howlers in Monkey River spend 1.5% of their time howling whereas they spend only 0.23% in RCNR (figure 8). A difference which is statistically significant (Mann-Whitney U-test: U=76.5, p=0.047).

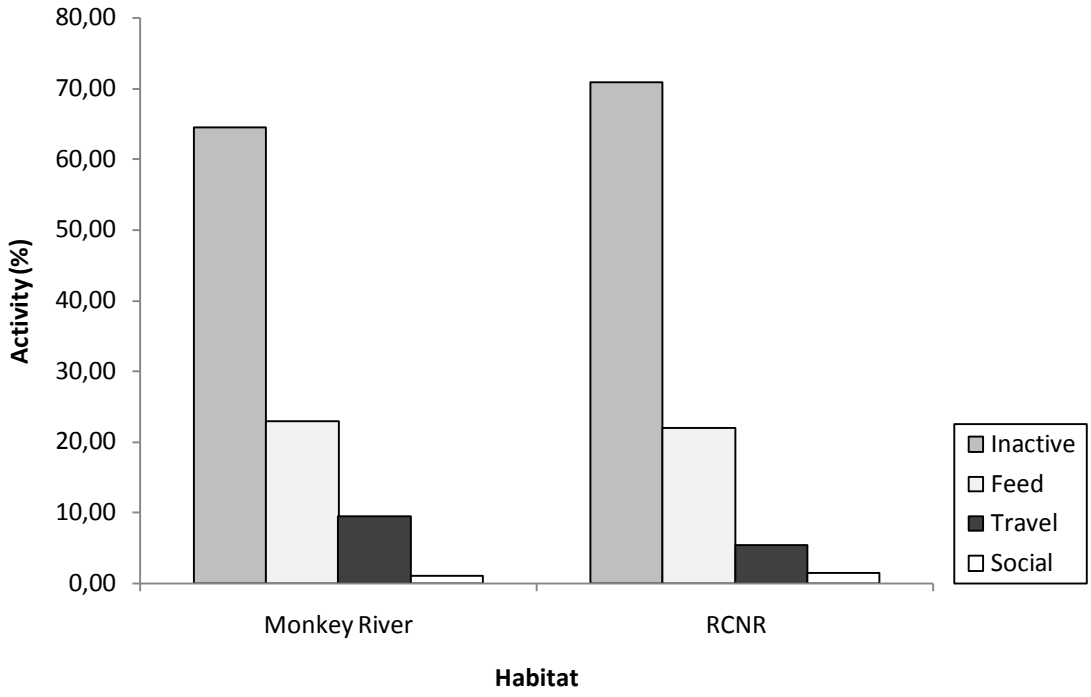

Figure 7. Activity budget of black howler monkeys in Monkey River and RCNR, Belize. Activity budget is categorized into Inactive, Feed, Travel and Social. Each activity is measured as percentage of time observed.

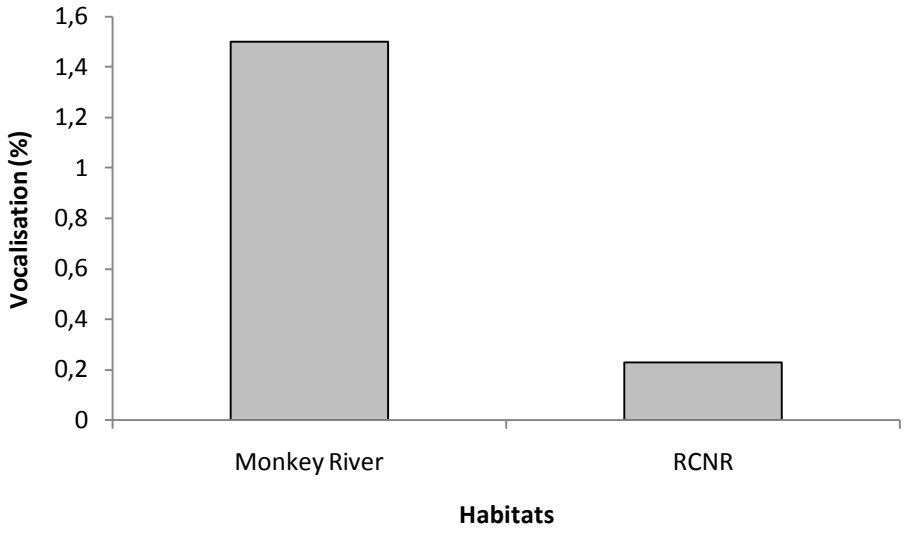

Figure 8. Amount of vocalisation measured as percentage of time observed for black howler monkeys in Monkey River and RCNR, Belize.

4. DISCUSSION

We asked ourselves what the differences between black howler monkeys populations living in disturbed riparian habitat with those living in undisturbed coastal limestone karst hills are. In a general way it appears that some aspects of their ecology show significant variations between the two populations while some others seem not to vary significantly, allowing us to discuss about how the studied variables actually influence each other and how relationships between ecological variables can be interfered.

We used the t-test and Mann-Whitney U-test to test for significant differences between the mean values of the ecological variables studied. The sample sizes used were pretty small. It is important to note that the p-value of a test depends on the sample size and that an important difference may not be statistically significant if the sample size is too small (Freedman *et al.*, 1998).

4.1. Food Availability

We predicted that food availability would be higher in Monkey River. According to the relative basal area of the food tree species, this prediction is confirmed when considering the most commonly eaten species accounting for 80% of the total feeding time and also when considering all the species from the diet.

However, it is important to note that the results obtained are underestimated as they do not include some food species because of their absence from the quadrats. Indeed, the vines, that account for 14.22% of the total feeding time in Monkey River and the vines and epiphyte (Philodendron), that account for 20.43% of the total feeding time in RCNR were not included in the quadrats. This is because they could not be analyzed with the same protocol as the one used for the species presenting an actual trunk, from which a basal area could be calculated. Moreover, one tree species in Monkey River and three tree species were not found in the quadrats probably because of their apparently low density in the forests. Thus, the higher percentage of vines and epiphytes eaten and the highest number of tree species not considered to calculate food availability in RCNR could partly account for the lower percentage of relative basal area of food tree species found.

4.2. Diet

We predicted that dietary diversity and plant diversity would be higher in RCNR due to the higher variation of ecological conditions at that site. Both of those predictions are well confirmed. The specific variations in topography of the karst hills offer a range of different environments and vegetations patterns (Crowther, 1982; Furley & Newey, 1979). This could explain the higher diversity of plant species found compare to Monkey River where the topography is more or less flat and where the chemical and physical composition of the soil is more homogeneous. Therefore one could expect to find a limited number of species of which chemical and physical needs are those offered by this homogenous riparian forest. However, it

is worth noting that the total number of species found in the quadrats in RCNR can be biased by the fact that the total sampling area in RCNR in larger of 0.64 ha than in Monkey River, leading eventually to a higher number of species sampled.

We suggest that the higher plant species diversity found in RCNR is very likely to explain the higher food sources diversity found in the diet. An increase in the number of food species could be an adaptation from the monkeys to their environment where food abundance is limited as this would allow them to get a relatively higher availability of food in their home range and allow the monkeys to travel less between food sources in order to meet their nutritional needs. But, the relatively low increase in total relative surface area resulting from the consumption of the 10 least eaten species compare to Monkey River suggest that a more diverse diet does not allow howlers to have a relatively higher food abundance in their home range. This suggests that howler's diet is closely linked with the diversity of species offered in the forest. The fact that the imprecise food categories "Fig" and "Vines" are likely to include different species may have biased this result. Indeed, it is possible that more species of fig can be part of howler's diet in Monkey River than in RCNR which would make their diet more diverse at the end. According to a study made in Monkey River, there were a total of 4 vines species in howler's diet before the hurricane and 3 after the hurricane (Behie & Pavelka, 2005) and a total of 4 vines species have been found in RCNR in the present study. Therefore, it is less likely that the category "Vines" in Monkey River includes more species than in RCNR but it is still imprecise and a potential source of bias.

When comparing both diets, it appears that slightly less species make up 80% of the diet in Monkey River meaning that monkey groups in Monkey River have a higher reliance on fewer species. Food species in both populations appear to be very different from each other according to the Sorensen's index of similarity, but this is not surprising as tree species composition varies greatly between the forests as also indicates Sorensen's index of similarity.

We also predicted howlers in Monkey River to spend more time feeding on fruits and flowers. This is partly confirmed as they do spend more time feeding on fruit but not on flowers. Those differences are not statistically different but there is more than 10% difference of the total feeding time on fruits between the two populations.

4.3. Population Density

We predicted that population density should be higher in Monkey River and the results obtained confirm this prediction. We suggest therefore that this relatively higher number of monkeys in the riparian forest is due to higher food availability which allows a larger population to subsist than in the limestone hills. It is interesting to note that despite the considerable decrease in food trees in the forest after the hurricane Iris, the howler population has been increasing, as is shown by the two fold increase in population density from 2004 to 2007 (Pavelka & Chapman, 2005).

The presence of spider monkeys in RCNR is also an important factor to underline as this competing species can reduce food availability and limit howler's energy intake. Thus,

food availability, as measured by the total relative basal area of food species, might not represent actual quantity of food available for the two howler populations proportionally as the population of spider monkeys in RNCR is very likely to diminish this food availability. We suggest that this sympatry may limit howler population growth and that is could have an influence on the lower population density found in the present study.

4.4. Group size and composition

We predicted mean group size to be higher in Monkey River and this prediction is confirmed, even if this difference is minimal. We suggest therefore that the higher population density in Monkey River tends to force howlers to live in larger groups, but the difference in mean group size between the two habitats is very little knowing that population densities are quite different. Other factors might therefore interfere this relationship. It is known that group composition is a function of group age, overall population growth and demographic events rather than food availability (Crockett, 1996) and thus indirectly population density. Indeed, a study made on different populations of *A. seniculus* firstly attributed differences in population parameters to the ecological variations between the two forests but further studies explained those differences were due to different stage of population growth (Crockett, 1984, 1985, 1996). Thus we can attribute the difference found in the present study not only to food availability and population density but also to historical event and population growth as we know hurricane Iris affected greatly the howler population (Pavelka *et al.*, 2007) as population density, mean group size and the number of groups have been considerably reduced for the following 3 years (Pavelka *et al.* 2007). Also, the decrease of the howler population in the entire forest fragment has also been found (Pavelka & Chapman, 2005). We can therefore suggest that space within the forest fragment including the 52-ha study site is still available, giving monkeys opportunities for dispersal and the formation of new groups and home ranges. This would keep mean group size at a certain level until the population size increases and get closer to carrying capacity and that howlers are force to stay in larger groups due to habitat saturation and less dispersal opportunities. It has been shown that it is more beneficial for males to disperse from multimale groups to create a new unimale group in a new home range rather than staying in such multimale group (Ostro *et al.*, 2001). Indeed, we found no multimale groups in Monkey River in the present study and there were 75% of multimale groups previous to the hurricane (Pavelka *et al.*, 2007). Thus higher food availability and population density in Monkey River might not be strong enough predictors of mean group size at time of the present study. Also, we found that population density almost doubled and mean group size increased by 30% between 2004 and 2007, suggesting the howler population to grow again and the forest to be recovering and potentially able to carry more monkeys in the future. Inversely, knowing that RCNR is a protected and pristine habitat that have moreover not suffer from the hurricane Iris, we can suggest the howler population there to be closer to the habitat's carrying capacity than the population in Monkey River. Thus, mean group size would be less likely to change in the future.

The results obtained regarding group composition does not fit our predictions. Firstly, the mean number of male per group was one in both habitats and there are therefore no

multimale groups in Monkey River but only heterosexual pairs and unimale-multifemale groups in both habitats. The formation of multimale groups may therefore not be the best alternative for males living in this forest as we discussed for group size. The prediction made that more infants per group should be present in Monkey River is also not confirmed. We predicted the presence of more adult males would protect infants against extragroup infanticide males (Treves, 2001; Van Belle & Estrada, 2008) but the results indicate there are not so many males. However, this can be attributed to the higher number of adult females per group in the forest with higher population density conditions. Indeed, larger female groups are known to be more attractive for invasive males which are likely to commit infanticide (Van Belle & Estrada, 2008; Crockett & Janson, 2000; van Schaik & Janson, 2000). The lower number of infants per groups could thus be the result of a higher level of infanticides from extragroup males as it has been suggested to occur in Monkey River soon after the hurricane (Pavelka *et al.*, 2003).

4.5. Home Range

Regarding home ranges, the results obtained confirm all the predictions made. Firstly, both home ranges reported in RCNR are larger than the 4 in Monkey River. The difference is not significant but it could be considered as quite important as on average, home range are more than eight hectares larger in RCNR. We suggest here that the higher food availability in Monkey River allows howlers to meet their nutritional needs over smaller area. Inversely, the lower food availability in RCNR forces howlers to feed over larger area. Moreover, during the entire study period, a considerable number of encounters between black howler monkeys and spider monkeys have been observed, confirming their strong sympatry in the forest. No aggressive interaction has been observed from either species. One time the dominant male of the group Hn has been observed howling as spider monkeys were travelling within 50 meters and the rest of the howler group including two females and four immature could not be detected in the periphery. On several occasions juvenile spider monkeys came relatively close to howler groups to start playing with immature howlers and no aggressive interactions were observed even when adults of each species encountered each other. Those behaviors show the lack of direct competition and possible aggressive relationship that could have been predicted between the two species. Moreover, it seems that in general howlers tend to be cryptic when they are foraging and that spiders are passing by. On few occasion, howlers have been seen to leave a foraging tree on the arrival of spider monkeys. Indeed, it has been noticed that they feed on some similar fruit species. Those observations may indicate the presence of indirect scramble competition over food in RCNR which is likely to occur at higher level than direct aggressive competition. Such competition is known to result in decreased foraging efficiency in a given patch (Terborgh & Janson, 1986) and therefore in an increase in home range size that can supply enough food for monkey groups (Dunbar, 1987; Chapman, 1988a, 1988b), which confirms the larger home ranges found in RCNR. We suggest also the higher population density in Monkey River force howlers to live in smaller home ranges. Ostro *et al.* (1999) showed that population density was inversely correlated to home range size for

A.pigra with higher population density in smaller home ranges. Other studies show that high densities of monkeys force groups to diminish their home ranges area due to the presence of competing neighboring groups (Dunbar, 1987; Dobson & Lyles, 1989).

It is important to note that home range sizes calculated for both habitats are likely to be underestimated as it has been measured on the basis of 4 consecutive months of study (dry seasons of the respective years) and it is likely that larger home range sizes can be observed with data collected over a longer period of time and especially when adding data from dry and wet seasons together. Those two distinct seasons can be associated with different patterns of food species availability and resulting habitat use. For example, a population of *A. seniculus* uses more often a reduced portion of their home range during a period of the year which contains the majority of the food trees (Palacios & Rodriguez, 2001). Another study shows that results on home ranges size of *A. pigra* more than doubled when studied during 1 year compared to 3 months (Ostro *et al.*, 1999). This is therefore something to take into account when comparing those home range sizes with those in other studies but this would have little effect on the present comparison as the data used for both habitats have been collected over the same length of time.

Secondly, the degree of overlapping is greater in Monkey River than in RCNR. We suggest that the population density being higher in Monkey River, howler groups would have to compete more for space pushing ranges to overlap with each other. Some studies have indeed found a relationship between population density and degree of overlapping between home ranges (Baldwin & Baldwin, 1972; Chivers, 1969; Crockett & Eisenberg, 1987). In study at Lamanai, were *A. pigra* population density is very high, Gavazzi *et al*. (2008) recorded a mean of 52% and up to 63% of overlapping between home ranges which is higher than in the present study. Depending on the carrying capacity of the forest of Monkey River, we can therefore expect to see the degree of overlapping increasing in the future if the population keeps growing. Inversely, the lower population density in RCNR allows howler monkeys to use widely their habitat, to progress over larger home ranges and find food without risking intraspecific aggressive interactions that is likely to occur in overlapping ranges. Non-overlapping home ranges have also been reported for a population of *A. seniculus* living at low population density and having large home ranges (Palacios & Rodriguez, 2001).

A study of howlers ranging behavior in RCNR over a longer period of time could show there is actually overlapping between the two groups studied. But because neither howler monkeys sightings nor howling have been recorded at close periphery of their home ranges, it is likely there is available space around Hn and Wn groups range and they would have the opportunity to expand their ranges in those areas if necessary, instead of overlapping their ranges and risking aggressive encounters.

4.6. Activity Budget

Regarding activity budgets, we predicted howlers in the limestone karst hills to spend more time travelling. This is not confirmed as monkeys in the riparian forest spend significantly more time traveling. We suggest that is in relation with their more frugivorous diet and the patchily distribution of fruits. Unfortunately, phenology data that would allow to

check for both a higher abundance of fruits in the dry season and a more patchily distribution of those fruits in Monkey River were not used for this study. Even if the differences in diet composition are not significant, there is still a trend and one could expect it to become significant if diet would be studied over a year (thus including the season of high fruit production which is not studied here). Indeed, diet, and the amount of fruits in the diet seem to affect time spent travelling and interacting socially: black howler monkeys spend more time travelling during periods of high fruit production and as a consequence, less time in social interactions (Pavelka & Knopff, 2004). This could be explained by the fact that monkeys obtain more energy from higher energy food or by the fact that they have to travel more in their home range as fruits are patchily distributed (Pavelka & Knopff, 2004). Similarly, studies on *A. palliata* shows that monkeys have longer daily ranges when fruit is abundant (Palacios & Rodrigues, 2001) and that an increase in fruits in the diet is followed by an increase in time spent traveling (Juan *et al.*, 2000). Thus, food abundance as measured in the present study, diversity of the diet and home range size seem not to be good predictor of traveling patterns in the present study.

Due to the predicted higher proportion of time spent traveling in RCNR we also predicted howlers to have less time available for resting. This prediction is not confirmed as howlers in Monkey River are more active, and even if the difference is not significant, this is probably due to their higher proportion of time traveling. Nevertheless, the insignificant difference suggests a lack of correlation between the level of frugivory and the level of inactivity, which confirms the conclusion made by Pavelka and Knopff (2004) in that the strong level of inactivity is not associated with howlers highly folivorous diet. We also predicted to observe more social interaction in Monkey River due to the presence of more infants (Behie & Pavelka, 2005). This prediction is not confirmed but the difference is not significant and indeed the difference is not important. Instead, howlers in RCNR spend more time in social interactions and this is probably due to the higher number of infants, which are thought to be the age class spending the highest amount of time in social play (Baldwin and Baldwin, 1978), and also to the fact they have more time available to spend in such interactions.

Finally, we predicted to observe more vocalizations in Monkey River. This prediction is confirmed as monkeys in the riparian forest spend significantly more time howling than those in RCNR. We suggest this is due to the higher percentage of overlapping between home ranges which might induce a stress to the socials groups. Inversely, neighboring groups in RCNR have exclusive home ranges during the dry season of the study so it is very unlikely that those groups could meet. This fits with the very low percentage of vocalization found, indicating they probably have no need to inform about their location in the forest and to regulate their distances. Such patterns confirm that vocalizations allow social groups to inform about their localizations to regulate their distance and prevent agonistic encounters (Carpenter, 1934; Chivers, 1969). Similarly, in a study on *A. paliatta* living at very low population density and in a very extensive home range with no overlap with other howler home ranges, Palacios & Rodriguez (2001) observed vocalizations at only 6 occasions during 10 months of study.

5. Conclusion and Perspectives

The fact that diets and tree species compositions in the two habitats are very different, confirm the flexible characteristic of howlers diet and their capacity to adapt their diet to the food available in their environment (Cristobal-Azkarate & Arroyo-Rodriguez, 2007; Silver et al., 1998). This is of important value considering the high rate of habitat loss and fragmentation and the need to protect remnant pristine habitats and primate populations. This is also interesting in the context of the secondary forest studied here. Indeed, in Monkey River, it appears that the black howler population is recovering from the strong harmful effect of the hurricane Iris. This is likely to be due to an increase in food availability and high quality food such as fruits compared to the years following the hurricane, resulting in an increase in group's reproductive success and overall increase in population growth. Then, the flexibility of howler's diet has allowed the population to survive with decreased food availability (Behie & Pavelka, 2005). Some population parameters such as group size seem not to be only influenced by population density as the small difference in mean group size between the two habitats does not seem to follow their respective population densities which differ more greatly. The effects of the hurricane on the howlers population can probably explain it as the habitat is probably not saturated and dispersal events, especially by males, are more common than before the hurricane which would allow, for a limited period of time, more and more groups to settle in the forest fragments while mean group size and mean number of males per group would remain moderate. Home ranges are larger in the limestone karst hills, which is likely due to the lower level of food available for the howlers. Food availability has been recorded to be lower there but it is also important to highlight the potential competition of spider monkeys which would make the amount of food available for howlers even lower. It is therefore interesting to note that food availability have been recorded to be higher in a disturbed forest than in an undisturbed forest, which gives a good point to the conservation value of secondary forests and fragmented habitats. Finally, activity budget seems to be influenced by different factors as the level of frugivory seem to affect directly the patterns of travel between fruit patches, thus time spent travelling and, the number of infants in groups seems to influence directly the amount of social interactions. Then, time spent inactive seems to be affected by time spent travelling. Finally, our results confirm that the amounts of vocalizations are associated with the need for howlers to announce their location to avoid encounters as both more vocalization and more overlapping have been recorded in Monkey River.

For further research in RCNR, it would be important to obtain more results on the entire primate community. Research on feeding ecology and social interactions, as well as on parasitism is now being done on Spider monkeys. Data on feeding ecology on the two sympatric primate species would allow us to assess the level of scramble competition over food between the two species. The assessment of indirect competition would also need phenology data in order to assess the availability in fruits and new leaves over time and space. Then it would be very interesting to use phenology data from the two habitats and analyze food availability over time and space to see if this is related to diet composition and eventually confirm the differences found in the present study. Also, data on social interactions

between the two species would allow us to understand better the patterns of howlers ranging behavior. In this goal, it would also be important to collect data on howler in RCNR over a longer period of time and especially to complete the data now available with those from the wet season. We could then obtain more complete home ranges estimates and eventually confirm there is no overlapping in RNCR. On a broader scale,

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7. APPENDIX

Appendix1: Ethogram

State behaviors:

Inactive - A default behavioral category that is used if an individual is not engaged in any activity. Behaviors include sitting, lying with eyes open, sleeping, or sun bathing.

Feed - The act of masticating, consuming, foraging among food sites, or drinking water. This broad category also includes the act of obtaining food such as reaching for a food item with the hands, feet or, mouth. Include details of the plant part and plant species being consumed.

Locomotion - Moving from one location to another in the same tree. Includes quadrupedal walking and running, bipedal walking and running, bridging, aided brachiating, leaping, and climbing upon a substrate.

Travel - Moving between trees.

Hang - An individual engaged in a behavior in which it is under the substrate to which it is supported by. This includes; using one to all four limbs and the prehensile tail.

Out of Sight - If the observer can no longer observe his or her focal animal this behavior is recorded. Samples in which the focal animal is not observable for a period of time exceeding one and a half minutes will be discarded.

Sit Near - Individuals that are within meter radius to the focal animal are recorded in this behavior.

Sit in Body Contact - Includes inactive activities in which the focal is in body contact with another animal. The following behaviors are encompassed; huddling, holding, licking, touching, lying in contact, and sitting in contact with another individual.

Ventral Cling - Infants that are clinging to a larger animal's (usually adults) ventrum for support. This behavior is intended for sessions when an infant is the focal animal. It doesn't take into account what behavior the larger animal is engaged in. For example, infants may cling to a moving or an inactive female. The behavior recorded remains "ventral cling". The moving female's behavior maybe recorded in the ad libitum notes

Dorsal Cling - This behavior uses the same pretence as the behavior above. An infant clinging to a larger animal's dorsal side for support is the requirement for this behavior.

Ventral Carry - This behavior focuses on the larger animal that is carrying a smaller infant on its ventral side. This behavior is intended when the focal animal is an adult or juvenile.

Dorsal Carry - Larger individuals who are carrying smaller infant on their dorsal side are engaged in the dorsal carry behavior. As above, this behavior is intended for adult or juvenile focal scans.

Copulation - This behavior is strictly focused on the act of sex. That is, the males penetration into a female's labia. It does not include dominant and submissive mounts.

Vocalization - Vocalizations can be categorized as either states or events. Any focal animal engaging in vocalizations that exceed 2 seconds are included in the state vocalization category. Such vocalizations include, grunts, and roars. This criteria, excludes alarm calls and barks.

Social Play - Individuals that engage in any play activity with another individual. Play behaviors include; wrestling, slapping, chasing others, play bites, pulling hair, and grabbing. Play behavior is a non-aggressive behavior and may include play faces and vocalizations.

Non-Social Play - Non-social play occurs when an individual is engaged in play behaviors alone. It is directed at infants, which constantly approach and leave another individual. This category includes behaviors such as playing with inanimate objects, or crawling upon other individuals who are inactive.

Scanning - Individuals who engage in this behavior are visually inspecting their environment. Scanning includes looking intensely at a particular object or looking to and fro in a general direction at a number of objects.

Vigilance - Vigilance is much like scanning, differing only in intensity and duration of the scan. Vigilance is characterized by an individual engaging in many short scans. Such behavior is observed when another group is near, a predator is near, or the individual is observing its group from afar. This behavior differs from scanning in intensity and context. Vigilance in this context is used as an alerted or cautious state.

Mount - Includes both males and females that mount the ano-genital area of another animal. Mounts are submissive and dominant in context. Both dorsal and ventral mounting may be recorded.

Embrace - This behavior is simply defined by an animal wrapping one or all four limps around another animal's dorsal or ventral side.

Allogroom - Any behavior in which the focal animal receives of initiates the following; inspect or combing through the hair of another individual, removing dead skin or parasites from another individual. Manipulation of hair may be preformed with theforelimbs and/or hind limbs.

Autogroom - All of the above behaviors, in which the individual directs its attention to itself as opposed to another individual.

Events:

Approach - This behavior may be initiated by the focal or received by another animal(s). It includes locomotion to another individual within a one-meter radius in any direction (Directed or Received).

Leave - The act of moving away from an animal with whom one has been SIB or SIN. (Directed or Received).

Displace - When the subject animal approaches another animal and that animal leaves. The subject then takes space formerly occupied by the displacee. (Directed or Received).

Muzzle - A behavior in which the focal animal rubs its face upon another animals face. Muzzling may also include kisses. (Directed or Received).

Lunge - Lunging occurs when an individual leaps or rapidly advances toward another monkey or animal. Lunges are agonistic behaviors that may or may not result in actual physical contact with the recipient. (Directed or Received).

Slap - Slapping is an agonistic behavior in which an animal strikes another animal with its' forelimb. (Directed or Received).

Branch Shake - Behavior in which the focal animal shakes a tree limb or branch. This apparently agonistic behavior is usually one component of an aggressive display directed toward another individual, another troop, or a researcher. Often branch shaking is accompanied with pilo erect hair.

Branch Throw - Behavior in which the focal animal breaks off a portion of a tree limb or branch and throws it at another individual. The recipient of the throw includes; another monkey from the same group, a monkey form a neighboring group, a potential predator, or a researcher.

Scratch - Characterized by the focal animal repeatedly rubbing or raking a portion of the body with its fingers. Scratching maybe preformed with the forelimbs, hind limbs, or tail. Scratching may relieve a skin irritation or remove invertebrates from a specific area. Excessive scratching in some cases is an abnormal behavior and may indicate an individual under a high degree of stress.

Elimination - A animal that is urinating or defecating.

Bridge - This event is characterized when an individual is between two substrates, holding both with hind limbs, fore limbs, and tail, in the process of crossing.

Quick Vocalization - A vocalization produced by an individual no longer than 2 seconds in duration. Quick vocalizations include; alarm calls, contact calls, and barks.

Unknown - This default category includes all behaviors that do not exist in the ethogram or cannot be identified by the researcher.

Appendix 2. List of the 42 species of plants found in quadrats and in howlers diet in Monkey River, Belize

Common name	Family	Genus and species name
Bathammons	-	-
Black Bay Cedar	Anacardiaceae	*Guazuma ulmfolia*
Breadfruit	-	-
Bullhorn Acacia*	Fabaceae	*Acacia cornigera*
Cabbage Bark*	Fabaceae	*Andira enermis*
Chicken toe	-	-
Chaparro[a]	-	-
Cochito	Myrtaceae	*Myriciara floribunda*
Cohune*	Palmae	*Attalea cohune*
Cojotone	Apocynaceae	*Stemmadenia donnell-smith*
Cotton tree	Bombaceae	*Ceiba pentandra*
Dogwood*	Fabaceae	*Lonchocarpus guatemalensis*
Fiddlewood*	Verbenaceae	*Vitex gaumeri*
Fig*	Moraceae	*Ficus sp*
Hog Plum*	Anacardiaceae	*Spondias mombin*
Inga	Fabaceae	*Inga edulis*
Swamp Kaway*	Fabaceae	*Pterocarpus officinalis*
Locust	Caesalpiniacaea	*Hymeneae courabil*
Mayflower	Bignoniaceae	*Tabebuia rosea*
Moho	Tiliaceae	-
Nectandra	-	-
Pokenoboy	Palmaea	*Sabal morrisiana*
Polewood	Anonaceae	*Xylopia frutescens*
Prickly Yellow*	Rutaceae	*Zanthoxylum kellermanii*
Provision	Bombaceae	*Pachira aquatic*
Red Gumbo Limbo*	Burseraceae	*Bursera simaruba*
Red Ramon*	-	-
Royal Palm	Arecaeae	*Roystonia regia*
Sering	Melastomaceae	*Miconia argentea*
Strangler Fig*	Moraceae	*Ficus crassiuscula*
Tama Tama Bri bri*	Fabaceae	*Inga*
Trumpet tree*	Moraceae	*Cecropia obtusifolia*
Turtle Bone*		
Vines*	-	-
White Gumbo Limbo*	-	-
Wild Breadnut		
Wild Cherry*		
Wild Custard Apple		
Wild Grape*	Polygonaceae	*Coccoloba belizensis*
Wild Lime	-	-
Yellow Bay Cedar		
Yemeri	Vochysiaceae	*Vochysia hondurensis*

*Species shared in the two habitats.

[a] Species that have been observed to be part of diet but not found in the quadrats.

Appendix 3. List of the 90 species of plants found in quadrats and in howlers diet in RCNR, Belize.

Common name	Family	Genus and species name
Accacia	Mimosoideae	*Acacia dolichostachya*
All Spice	Myrtaceae	*Pimienta dioica*
Ball Seed tree	Fabaceae	*Andira enermis*
Barba Jolete	Mimosaceae	*Cojoba arborea*
Bastard Rosewood	Fabaceae	*Swartzia cubensis*
Bay Leaf Palm	Arecaea	*Sabal mauritiiformis*
Billy Webb	Fabaceae	*Acosmium panamese*
Bitterwood	Simaroubaceae	*Picraena excela*
Black Poisonwood	Anacardiaceae	*Metopium brownei*
Black Sapote	Anacardiaceae	*Metopium brownie*
Boyjob/Wild Kinep	Sapindaceae	*Matayba apetala-*
Broadleaf Moho	Tiliaceae	*Heliocarpus americanus*
Bri bri type	Mimosoidaea	*Inga*
Male Bull Hoof	Euphorbiaceae	*Drypetes browneii*
Bullet Tree	Combretaceae	*Bucida buceras*
Bullhorn Accacia*	Fabaceae	*Acacia cornigera*
Candlewood	Dracaenaceae	*Dracaena americana*
Cabbage Bark*	Fabaceae	*Andira enermis*
Carbone del rio	Meliaceae	*Trichilia palida*
Cocoloba B.	-	-
Cocoloba sp.	-	-
Cohune Palm*	Palmae	*Attalea cohune*
Copal	Burseraceae	*Protium copal*
Copna[a]	-	-
Kopac	Bombacaceae	*Pseudobombax ellipicum*
Creamwood	Sapotaceae	*Sideroxylon floribundum*
Dandruff Wood	Flacourtiaceae	*Zuelania guidonia-*
Dog Tone	Apocynaceae	*Thevetia ahouai*
Dogwood*	Fabaceae	*Lonchocarpus guatemalensis*
Dogballs	-	-
Drancoredwood	-	-
Fiddlewood*	Verbenaceae	*Vitex gaumeri*
Fig*	Moraceae	*Ficus sp.*
Franjipani	Apocynaceae	*Plumeria sp.*
Give and Take	Palmae	*Crysophila argentea*
Glassywood	Rubiaceae	*Guettarda combsii*
Grandy Betty	Sapindaceae	*Cupania Belizensis*
Guayavillo	Myrtaceae	*Eugenia*
Gaussia maya	Arecaceae	*Gaussia maya*
Hog Plum*	Anacardiaceae	*Spondias mombin*
Horse Balls	Apocynaceae	*Spondias mombin*
Hyper Lucia	-	-
Ironwood	Fabaceae/Caesalpinoideae	*Dialium guianense*
Jobillo	Anacardiaceae	*Astroneum graveolens*
John Crow Redwood	Rubiaceae	*Simiria salvadorensis*
Swamp Kaway*[a]	Fabaceae	*Pterocarpus officinalis*

Mahogany	Meliaceae	*Swietenia macrophylla*
Lycher Maria	-	-
Mammee Cirela	Sapotaceae	*Pouteria durlandii*
Mountain Moho	Tiliaceae	*Luhea speciosa-*
Red Mylady	Apocynaceae	*Aspidosperma cruentum*
Nargusta	Combretaceae	*Terminalia amazonia*
Narrow Leaf Moho	Tiliaceae	*Trichospermum grewiifolia*
Negrito	Simaroubaceae	*Simarouba glauca*
Paletillo	Flacourtaceae	*Casaeria corymbosa*
Pigeon Plum	Chrysobalanaceae	*Hirtella americana*
Philodendron[a]	-	-
Polewood	-	-
Prickly Yellow*	Rutaceae	*Zanthoxylum kellermanii*
Quamwood	Fabaceae	*Schizolobium parahyba*
Rain Tree	Fabaceae/Mimosoideae	*Samanea saman*
Red Ramon*	Moraceae	*Trophis racemosa*
Red Silion	Sapotaceae	*Pouteria amygdalina*
Red Gumbolimbo*	Burseraceae	*Bursera simaruba*
Rubber tree	-	-
Sam Wood	Boraginaceae	*Cordia alliodora*
Santa Maria	Guttiferae	*Calophyllum brasiliense*
Sapodilla	Sapotaecae	*Manilkara zapota*
Shippia Palm	Aracaeae	*Shippia concolor*
Soap Tree	Sapindaceae	*Sapindus saponaria*
Strangler fig*	Moraceae	*Ficus crassiuscula*
Swiddlewood	Boraginaceae	*Cordia diversifolia*
Tamatama Bribri*	Fabaceae	*Inga*
Tiger Bay Leaf Palm	Arecaceae	*Sabal*
Timbersweet		
Trumpet tree*	-	-
Turtle Bone*	Fabaceae	-
Warrie Wood	Fabaceae	-
Water Wood	Rhizophoraceae	-
Welliam[a]	-	-
Vines[a]	-	-
White Gumbolimbo*	-	-
White Cabbage Bark	Fabaceae	*Lonchocarpus minimiflorus*
White My Lady	Apocynaceae	*Aspidosperma megalocarpon*
White Poisonwood	Apocynaceae	*Cameraria*
Wild Breadnut*	Moraceae	*Brosimum alicastrum*
Wild Cherry*	Moraceae	*Pseudomeldia spuria*
Wild Coffee	Violaceae	*Rhinorea*
Wild Grape*	Polygonaceae	*Coccoloba belizensis*
Wild Guava	Myrsinaceae	*Ardisia*
Wild Mammee	Rubiaceae	*Alseis yucatanensis*

*Species shared in the two habitats.

[a] Species that have been observed to be part of diet but not found in the quadrats.

Appendix 4. Groups size and compositions for black howlers populations in Monkey River and Belize.

Habitat	Group	Adult F	Adult M	Sub F	Sub M	Juv	Infant	Group size	Sex ratio
Monkey River	Q	1	1	0	0	2	0	4	(1:1)
	A	1	1	0	0	1	0	3	(1:1)
	B	2	1	0	1	1	1*	6	(1:2)
	N	1	1	1	0	2	1*	6	(1:1)
	G	3	1	0	1	1	1*	7	(1:3)
	Total	***8***	***5***	***1***	***2***	***7***	***3***	***26***	***(5:8)***
	Mean	***1.6***	***1***	***0.2***	***0.4***	***1.4***	***0.6***	***5.2***	***(1:1.6)***
RCNR	Hn	2	1	0	0	2	2	7	(1:2)
	Wn	1	1	1	0	0	1*	4	(1:1)
	Mn	1	1	0	1	1	0	4	(1:1)
	Total	***4***	***3***	***1***	***1***	***3***	***3***	***15***	***(3:4)***
	Mean	***1.3***	***1***	***0.3***	***0.3***	***1***	***1***	***5***	***(1:1.3)***

* infants that were born during the study period.